Coral Reefs (2005) 24: 594–602
DOI 10.1007/s00338-005-0031-3

REPORT

Rhian G. Waller · Paul A. Tyler · John D. Gage

Sexual reproduction in three hermaphroditic deep-sea *Caryophyllia* species (Anthozoa: Scleractinia) from the NE Atlantic Ocean

Received: 7 July 2005 / Accepted: 7 July 2005 / Published online: 24 September 2005

Abstract The reproductive biology and gametogenesis of three species of *Caryophyllia* were examined using histological techniques. *Caryophyllia ambrosia*, Alcock 1898, *C. cornuformis*, Pourtales 1868, and *C. sequenzae*, Duncan 1873, were collected from the Porcupine Seabight and Rockall Trough in the NE Atlantic Ocean. These three ahermatypic solitary corals inhabit different depth ranges: *C. cornuformis* – 435–2000 m, *C. sequenzae* – 960–1900 m, and *C. ambrosia* – 1100–3000 m. All three species are hermaphroditic. Hermaphroditism in these species was found to be cyclical, with only one sex of gametes viable in any individual at any point in time, although gametes of both sexes were found together within a single mesentery. Once the viable gametes are spawned, the next sex of gametes continues to grow until mature, and so gametogenesis is a continuous cycle. Oocytes and spermacysts in all species increased in density towards the actinopharynx. Maximum fecundity for *C. sequenzae* was 940 oocytes per polyp, and for *C. ambrosia* 2900 oocytes per polyp. Fecundity could not be established for *C. cornuformis*. In all three species, individuals were asynchronous within populations, and production of gametes was quasi-continuous throughout the year. All species are hypothesised to have lecithotrophic larvae owing to their large oocyte sizes (*C. cornuformis* max – 350 μm; *C. sequenzae* max – 430 μm; *C. ambrosia* max – 700 μm). Both the average oocyte size and fecundity increased in species going down the depth gradient of the NE Atlantic.

Keywords Ahermatypic · Azooxanthellate · Solitary coral · Gametogenesis · Cyclical hermaphrodite

Communicated by Environmental Editor B.G. Hatcher

R. G. Waller (✉)
Woods Hole Oceanographic Institution,
MS#33, 2-14 Redfield, Woods Hole, MA 02543, USA
E-mail: rwaller@whoi.edu
Tel.: +1-508-2893761
Fax: +1-508-4572134

P. A. Tyler
Southampton Oceanography Centre, European Way,
Southampton, SO14 3ZH, UK

J. D. Gage
Scottish Association for Marine Biology,
Dunstaffnage Marine Laboratory, Oban, Argyll,
PA, 34 4AD, UK

Introduction

Deep-water scleractinian corals are both diverse in morphology and cosmopolitan, being found in all the world's oceans (Zibrowius 1980). Species are either colonial reef-builders or occur as solitary polyps, with reef-building species forming important habitats for numerous invertebrate and vertebrate species, many of increasing commercial value (Rogers 1999; Mortensen 2000). Deep-water solitary species are more diverse in morphology, can inhabit both sedimented and rocky substrata, and have been found at greater depths than reef-builders (Cairns 1979; Zibrowius 1980).

Species in the phylum Cnidaria show varying combinations of reproductive patterns—sexual, asexual, free-spawning, brooding, external fertilisation, internal fertilisation, gonochorism, hermaphroditism, seasonal, continuous and periodic life histories have all been found in this diverse group (Fadlallah 1983; Harrison and Wallace 1990). The Scleractinia are typical of this variety. Most information on coral reproduction is derived from studies of shallow-water species, whilst only four reports thus far have described reproduction in deep-water scleractinians. Waller et al. (2002) examined the gametogenic biology of *Fungiacyathus marenzelleri* from the Rockall Trough (NE Atlantic). Brooke (2002) reported on the reef builder *Oculina varicosa* from the east coast of Florida. Waller and Tyler (in press) studied the reef builders *Lophelia pertusa* and *Madrepora oculata* from a variety of sites in the NE Atlantic Ocean, and Burgess and Babcock (2005) examined *Enallopsammia rostrata*, *Solenosmillia variabilis*, *Goniocorella dumosa*, and *Mad-*

repora oculata from the Chatham Rise. *F. marenzelleri* and *E. rostrata* are non-seasonally breeding gonochoric species; *O. varicosa*, *L. pertusa*, *S. variabilis*, and *G. dumosa* are seasonal gonochoric species; and *M. oculata* is a periodic gonochoric species. Six of these species appear to have oocyte sizes that indicate lecithotrophic larval development, with *O. varicosa* being the exception.

Additional information is available on the reproductive ecology of other deep-water anthozoans. Van Praet et al. (1990) described the gametogenic biology of two actinarian species of the genus *Phelliactis*. Bronsdon et al. (1993) described reproductive processes in the actinarian epizoites,*Amphianthus inornatus* and *Kadosactis commensalis*. Muirhead et al. (1986) observed gametogenesis in two Epizooanthus species, the bathyal *E. paguriphilus* and the abyssal *E. abyssorum*. In the Alcyonaria, Rice et al. (1992) and Tyler et al. (1995) described the gametogenic patterns for a variety of deep-water pennatulids.

The pattern of reproduction has also been described for several shallow-water solitary corals, of which the majority are gonochoric, brooding species (Fadlallah 1983). *Balanophyllia elegans* is a non-seasonal brooder (Fadlallah and Pearse 1982a) and *Paracyathus stearnsii* is a seasonal spawner (Fadlallah and Pearse 1982b). *Fungia scutaria* is gonochoric and spawns gametes during the late summer (Krupp 1983), whilst Goffredo et al. (2000, 2002) observed *Balanophyllia europaea* to be a hermaphroditic brooder. The reproductive biology is also known for two shallow-water species of *Caryophyllia*. The Devonshire Cup Coral, *Caryophyllia smithii*, can be found around the British coast (as well throughout the Atlantic) from just a few metres depth to over 1200 m (Zibrowius 1980). Shallow *C. smithii*, a gonochoric seasonal reproducer, spawns gametes during March, and produces a planktotrophic larvae (Tranter et al. 1982), though there are reports of brooding in this species (Hiscock and Howlett 1977). *Caryophyllia clavus* also broods its young, though little else is known (Fadlallah 1983).

In this paper we report on the gametogenic development and fecundity of three deep-water *Caryophyllia* inhabiting different, but overlapping, depth ranges in the NE Atlantic Ocean. *C. ambrosia* (Fig. 1a) lives between 1100 and 3000 m depth, *C. sequenzae* (Fig. 1b) lives between 960 m and 1900 m depth, whilst the most shallow species, *C. cornuformis* (Fig. 1c), lives between 435 and 2000 m (Zibrowius, 1980). *C. ambrosia* is the most cosmopolitan of these three species, occurring in the Atlantic, Pacific, and Indian Oceans. *C. cornuformis* has been found at numerous locations around the Atlantic, and *C. sequenzae* has only been found in the Eastern Atlantic.

This study is part of the interdisciplinary European project 'Atlantic Coral Ecosystem Survey' (ACES). This project began in April 2000 to examine the biology, oceanography, and geology of scleractinians at bathyal depths round the European margin.

Methods

Samples were collected by either 5 m Agassiz beam trawl or Otter Trawl Semi-Balloon (14 m) from the research vessels RRS *Challenger*, RRS *Charles Darwin*, and RRS *Discovery* between 1978 and 2002 (Table 1). Samples of *C. cornuformis* were collected from the Porcupine Seabight and the Rockall Trough. The material was preserved in 4% formalin and later transferred to 70% alcohol. Before histological preparation, all individuals were submerged for approximately 4 h in rapid decalcifying solution (conc. HCL) until no carbonate skeleton remained. They were then rinsed in running tap water for 24 h to remove acid traces. Polyps were then wet-weighed prior to dissection. After decalcification, mesenteries from 20 whole individuals of each species (collected in different seasons) were counted and their structure noted.

For histological preparation, the whole polyps of *C. cornuformis* and 3 mesenteries of each of 15 individuals of *C. sequenzae* and *C. ambrosi*a were dehydrated by three, 4-h, submersions in 100% propan-2-ol, followed by clearing with xylene for approximately 12 h. These were then embedded by being left for 6–12 h in molten histology wax at 70°C and poured into standard moulds. All wax blocks were serially sectioned at 5 μm, leaving 50 μm in between slides, and stained with Masson's Trichrome stain.

Sections of each individual were then examined using an Olympus BH2 compound microscope with video camera attachment. Images were captured using Matrox Rainbow Runner and analysed using SigmaScan Pro version 4 to calculate oocyte diameters. 'Feret' diameter

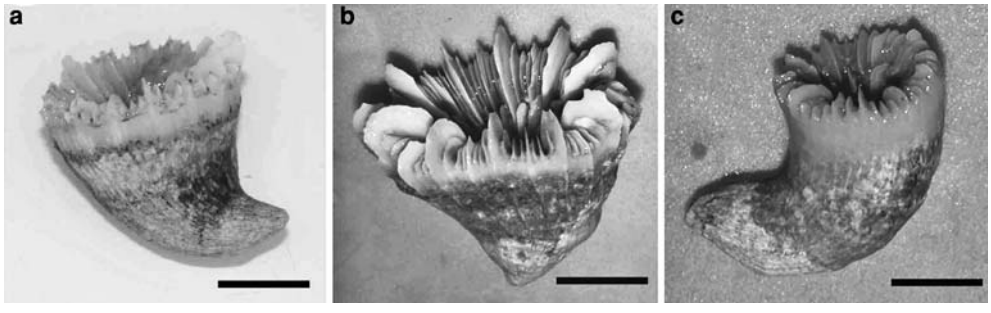

Fig. 1 Specimens of three deep-sea, solitary scleractinian corals from the NE Atlantic, **a** *Caryophyllia cornuformis*; **b** *C. sequenzae*; **c** *C. ambrosia* *Scale bars* = **a** 1 cm; **b** 2 cm; **c** 2 cm

Table 1 Details of deep-water *Caryophyllia* species sampled for this study in the NE Atlantic Ocean

Species	Date	Vessel	Depth	Latitude/longitude
C. sequenzae	12.2.98	RRS *Discovery*	1278 m	58° 58′ N 07°′57 W
	24.4.78	RRS *Discovery*	1404 m	50° 30′ N 12°00′ W
	7.11.80	RRS *Darwin*	1250 m	51° 04′ N 11°50′ W
	19.10.02	RRS *Discovery*	1240 m	49° 50′ N 12° 05′ W
C. ambrosia	20.6.85	RRS *Darwin*	2440 m	51° 00′ N 12° 59′ W
	4.8.81	RRS *Challenger*	2713 m	51° 05′ N 11° 48′ W
	21.3.02	RRS *Discovery*	2500 m	49° 36′ N 12° 11′ W
	4.9.79	RRS *Discovery*	2315 m	51° 00′ N 12° 03′ W
	1.10.02	RRS *Discovery*	2452 m	50° 04′ N 12° 45′ W
C. cornuformis	10.3.93	RRS *Challenger*	1650 m	57° 07′ N 09° 30′ W
	11.8.92	RRS *Darwin*	2017 m	57° 00′ N 09° 58′ W

(the area if the oocyte was a perfect circle) was used as this normalises the often irregular outline of the oocytes that results from close packing in the mesentery. 'Plymouth Routines in Multivariate Ecological Research'(PRIMER) 5 was used to statistically analyse and allow grouping of oocyte size-frequency data. Multidimensional Scaling (MDS) and Analysis of Similarity (ANOSIM) were also used. Spermatogenesis and oogenesis were staged.

To estimate fecundity, all female and hermaphroditic slides were examined. All previtellogenic, vitellogenic, and late vitellogenic oocytes were counted in three mesenteries from each female. The number of oocytes in the three mesenteries were averaged (realised fecundity), then multiplied by the total number of mesenteries within the individual (potential fecundity).

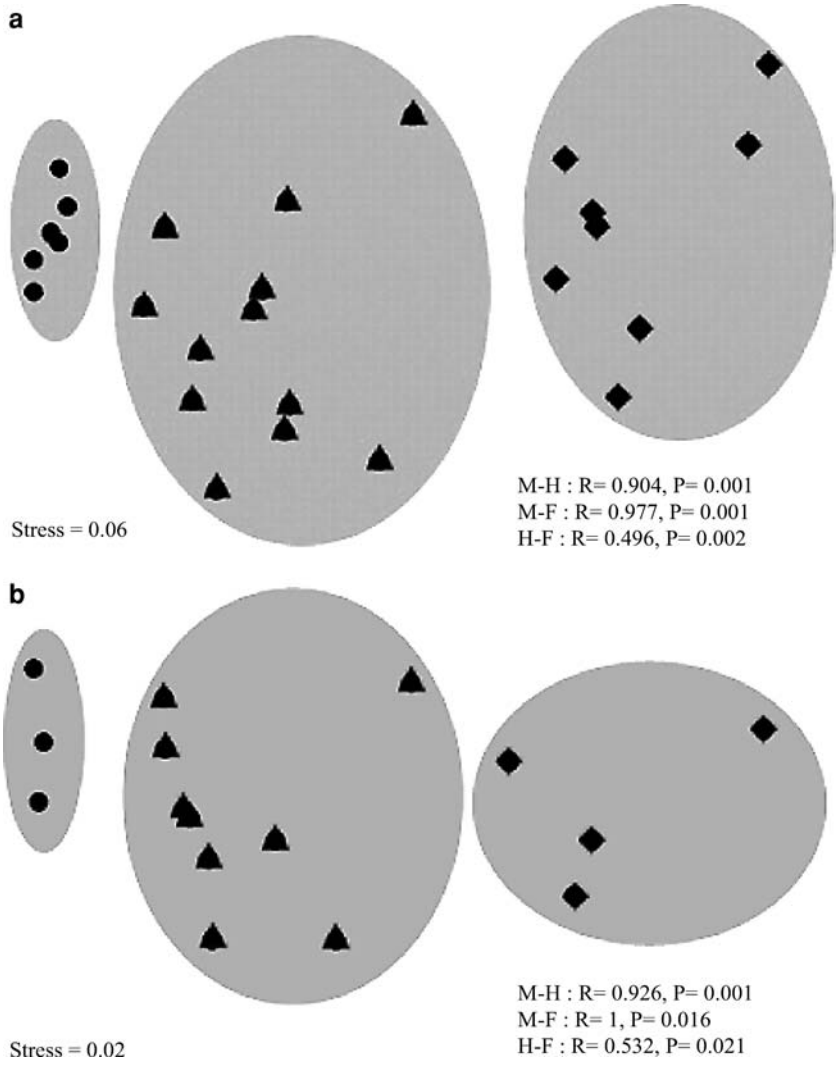

Fig. 2 PRIMER MDS plot and ANOSIM statistics of oocyte size (feret diameter μm) for (**a**) *C. ambrosia* and (**b**) *C. sequenzae*. *Circles*, female hermaphrodites; *triangles*, intermediate; *diamonds*, male hermaphrodites. M-H, male-hermaphrodite; M–F, male–female; H-F, hermaphrodite-female

Results

Gametogenesis in the genus *Caryophyllia*

Caryophyllia ambrosia

Five monthly samples were available for analysis. *C. ambrosia* is a cyclical hermaphroditic, where one sex appears to be dominant at any one time. Individuals are termed 'female' and 'male' hermaphrodites, according to the dominant sex (with 'Intermediate' used to describe those containing gametes of both sexes at similar stages of development). PRIMER MDS and ANOSIM analysis (Fig. 2) show the three groupings to differ significantly from each other ($R > 0.496$; $p > 0.001$). Gametes of both sexes develop from the mesenterial lamellae (Fig. 3a). Both male and female gametes were found in several clusters throughout the same mesentery and increased in density towards the actinopharynx.

Oogenesis Oogenesis can be divided into four stages: Stage one—Oogonia (< 50 μm) are observed budding from the mesenterial lamellae; Stage two—Previtellogenic oocytes (< 250 μm) containing a large nucleus (Fig. 3a); Stage three—Vitellogenic oocytes (< 500 μm) showing evidence of rapid yolk accumulation (Fig. 3b, c); and Stage four—Late Vitellogenic oocytes (> 500 μm) that have a thick cortical granular layer just inside the oolemma, and large yolk granules and prominent nucleolus in the central nucleus (Fig. 3d)

Oocytes within a single individual were at the same stage of development, whereas individuals from the same sample showed asynchrony in oocyte development. Oocyte size-frequency diagrams show this asynchrony

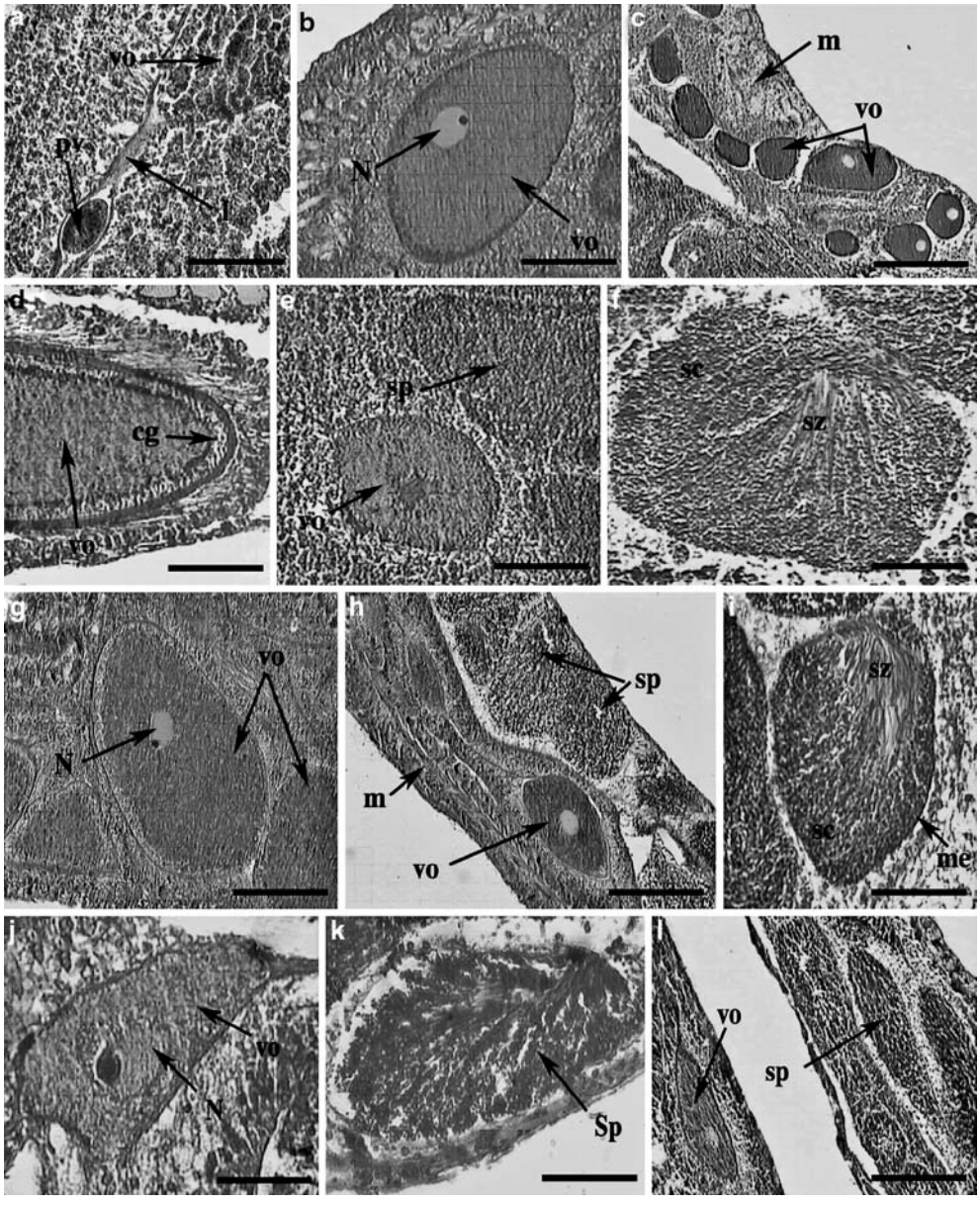

Fig. 3 **a** *C. ambrosia* previtellogenic and vitellogenic oocytes connected by the mesenterial lamellae. **b** *C. ambrosia* vitellogenic oocyte. **c** *C. ambrosia* female mesentery. **d** *C. ambrosia* late vitellogenic oocyte showing cortical granular layer. **e** *C. ambrosia* hermaphroditic mesentery. **f** *C. ambrosia* stage III spermacyst. **g** *C. seguenzae* vitellogenic oocytes. **h** *C. seguenzae* hermaphroditic mesentery. **i** *C. seguenzae* stage III spermacyst. **j** *C. cornuformis* vitellogenic oocyte. **k** *C. cornuformis* stage III spermacyst. **l** . *C. cornuformis* hermaphroditic mesenteries. *pv*, previtellogenic oocyte; *vo*, vitellogenic oocyte; *l*, mesenterial lamellae; *N*, nucleus; *m*, mesentery; *cg*, cortical granular layer; *sp*, spermacyst; *sc*, spermatocytes; *sz*, spermatozoa; *me*, mesogleal envelope. *Scale bars* = **a**, 200 μm; **b**, 200 μm; **c**, 400 μm;**d**, 100 μm; **e**, 200 μm;**f**, 100 μm, **g**, 100 μm; **h**, 200 μm; **i**, 100 μm, **j**, 50 μm; **k**, 50 μm; **l**, 100 μm

and the unimodal development of oocytes (Fig. 4). The maximum oocyte diameter observed was 700 µm. Hermaphroditic individuals (Fig. 3e), containing developing oocytes, were found in all sizes of polyp.

Spermatogenesis Four stages of spermatogenesis were identified: Stage one (early)—loosely packed aggregations of spermatocytes contained within a spermacyst empty lumen can be observed; Stage two (maturing)—some spermatozoa are present, starting to fill the lumen but loosely packed; Stage three (mature)—well-developed spermatocyte layer and lumen packed with spermatozoa (Fig. 3f); and Stage four (spent)—relict spermatozoa can be seen.

Spermacysts were observed to be in a similar stage of development within a single individual. Hermaphrodites that were predominantly female had fewer, smaller spermacysts, at earlier stages, than male hermaphrodites.

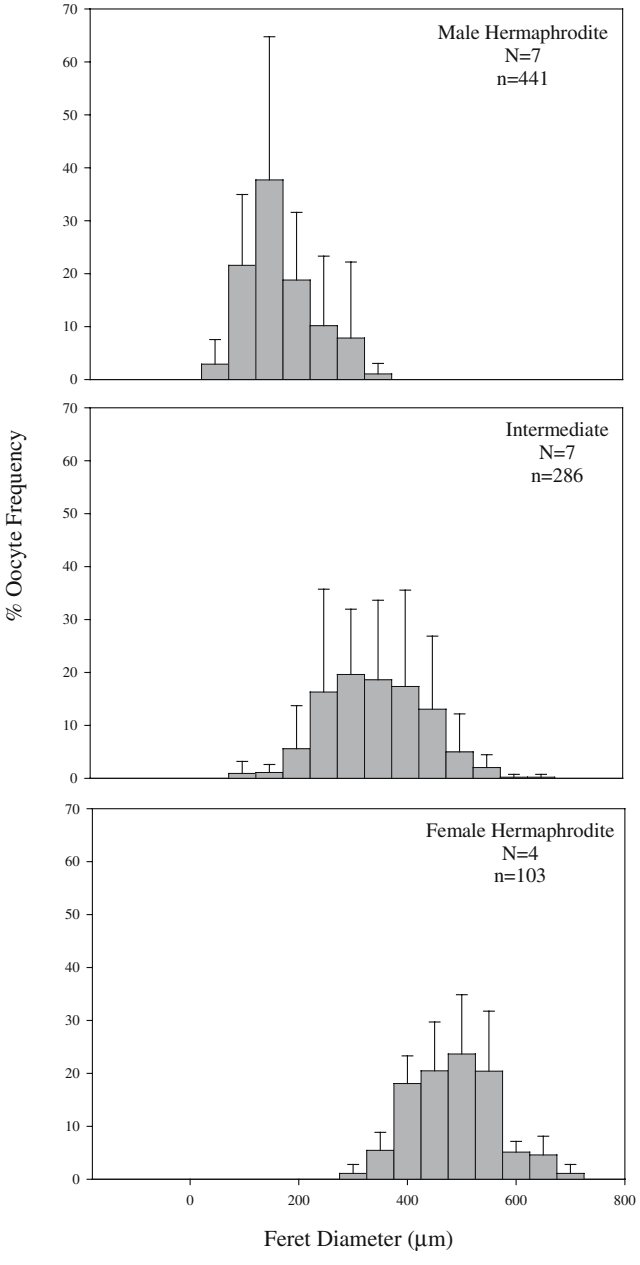

Fig. 4 Oocyte size-frequency distribution plots for *C. ambrosia*. Plots split into 'male hermaphrodites', 'intermediate' and 'female hermaphrodites' using PRIMER (see Fig. 2). *Error bars* = ±1SD; *N* = number of individuals; *n* = number of oocytes measured

Caryophyllia sequenza

Four monthly samples were analysed during this study. *C. sequenzae* is also a cyclical hermaphrodite, as is *C. ambrosia*. Separate male, female, and intermediate hermaphroditic individuals were again statistically identified (PRIMER MDS and ANOSIM, Fig. 2, $R > 0.532$; $p > 0.001$) (Fig. 2). Gametes of both sexes develop from the mesenterial lamellae. Both male and female gametes were found in several pockets throughout the same mesentery, and increased in density towards the actinopharynx.

Oogenesis Oogenesis is very similar to that of *C. ambrosia*, with differing oocyte sizes: Stage One—ovoid oogonia are < 60 µm; Stage two—previtellogenic oocytes are < 125 µm; Stage three—vitellogenic oocytes are < 350 µm (Fig. 3g); Stage four— late vitellogenic oocytes are > 350 µm reaching a maximum size of 450 µm

Oocytes within a single individual were at a similar stage of development, whereas individuals from the same sample showed asynchrony in oocyte development. Oocyte size-frequency diagrams show this asynchrony and the unimodal development of oocytes (Fig. 5). The maximum oocyte diameter observed was 450 µm. Hermaphroditic individuals, containing developing oocytes, were found in all sizes of individual polyp (Fig. 3h).

Spermatogenesis Spermatogenesis in *C. sequenzae* follows the same stages as *C. ambrosia*. Spermacysts were observed to be in a similar stage of development within a single individual and, as in *C. ambrosia*, these were mainly late stages (Fig. 3i). Hermaphrodites that were predominantly female had fewer, smaller spermacysts, at earlier stages, than male hermaphrodites.

Caryophyllia cornuformis (Fig. 3j, k, l)

Only two monthly samples of this species were obtained, and they were not in good condition. It is thought that formalin penetration into the lower extremities was poor, and so tissue was not preserved adequately to gain reliable fecundity estimates or numerous measurements of oocyte diameter.

This species is also a hermaphrodite, which may also be cyclical, though insufficient samples were available for a conclusive assessment. There were insufficient oocytes in measurable condition to develop oocyte size-frequency histograms for this species, and so sizes were averaged for every individual and then for the two

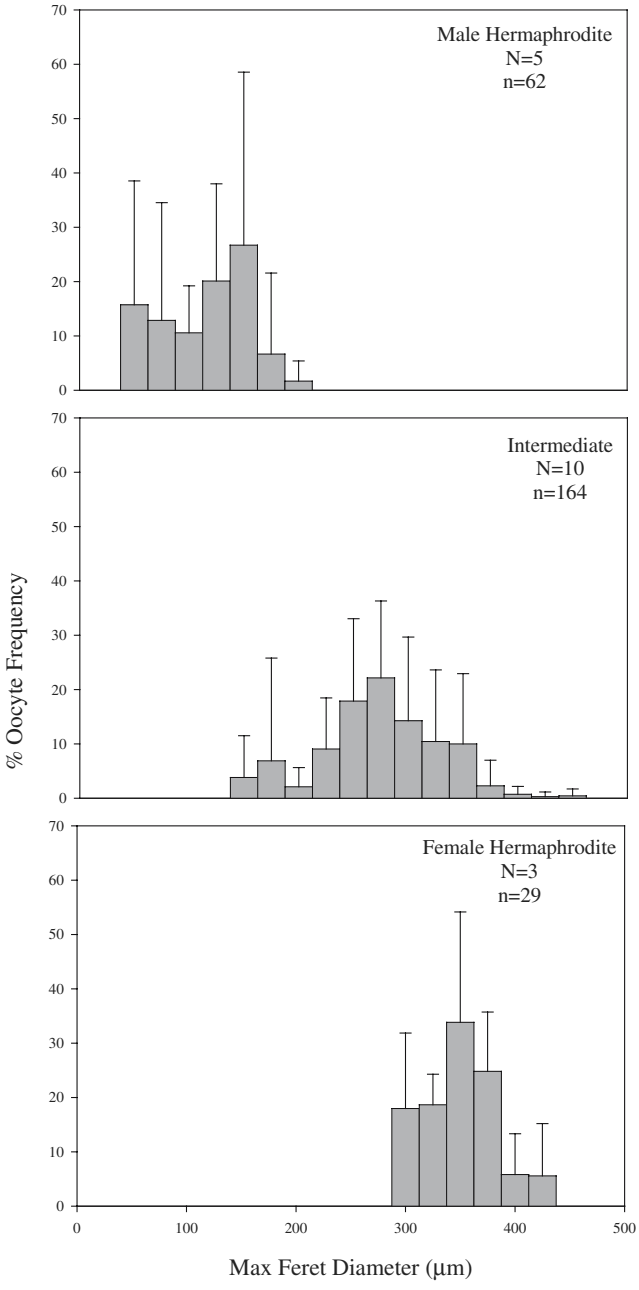

Fig. 5 Oocyte size-frequency distribution plots for *C. seguenzae*. Plots split into 'male hermaphrodites', 'intermediate' and 'female hermaphrodites' using PRIMER (see Fig. 2). *Error bars* = ±1 SD; *N* = number of individuals; *n* = number of oocytes measured

sample months (Fig. 6). Maximum oocyte size is 350 µm. Individuals from the same sample had varying average oocyte diameters.

Fecundity

Fecundity was calculated from both 'female' and 'male' hermaphrodites in both *C. ambrosia* and *C. sequenzae*. There was no significant difference in realised fecundity between these two phases in either species (*C. ambrosia*—$U = 43.5$, $p = 0.078$; *C.seguenzae*—$U = 36.0$, $p = 0.2986$).

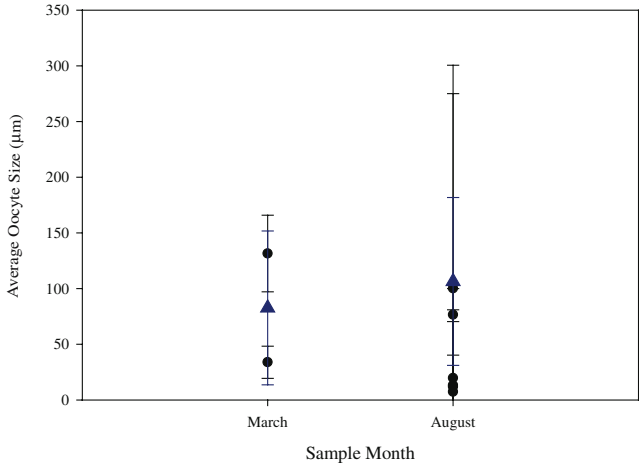

Fig. 6 Average oocyte diameters in *C. cornuformis* sampled in March 1993 and August 1992 from the N.E. Atlantic Ocean. *circles*, individual average oocyte diameters; *triangles*, average oocyte diameter for a month; *error bars* = ±1 SD

C. ambrosia

Potential fecundity was calculated as a minimum of 200 oocytes per polyp and a maximum of 2750 oocytes per polyp. After size correction there was no significant difference in average fecundity analysed among the four months ($U = > 8.5$, $p = > 0.155$), indicating nearly continuous production of gametes over this period. Fecundity did not increase with wet weight of polyp ($r^2 = 0.227$; $p = 0.05$), and there was no distinct size of first reproduction within the size range of individuals observed.

C. seguenzae

Potential fecundity was calculated at a minimum of 52 oocytes per polyp and a maximum of 940 oocytes per polyp. After size correction, there was no significant difference in average fecundity analysed among the four months ($U = 54$, $p = 0.006$), suggesting a quasi-continuous production of gametes.

Fecundity is size-dependent (Fig. 7; $r^2 = 0.728$; $p < 0.05$). Non-reproducing individuals were not included in the regression, as there was no distinct size of first reproduction.

Discussion

All three of these deep-water scleractinians show asynchronous, cyclical hermaphroditism with no evidence of seasonality. The majority of scleractinians, for which the patterns of reproduction is known, are hermaphroditic (Fadlallah 1983; Harrison et al. 1984; Szmant 1986),

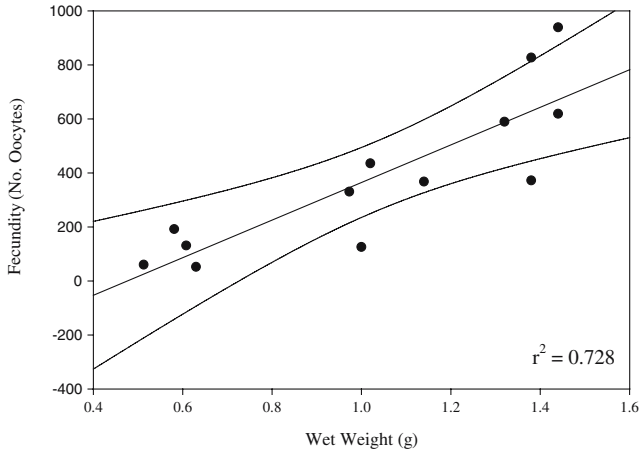

Fig. 7 Realised fecundity (# oocytes) plotted against polyp wet weight (g) of *C. sequenzae*, fitted with linear regression. N = number of individuals; $N = 13$; 99% confidence intervals; $f = y0 + a*x$; Size corrected to 1.398 g polyp wet weight

with this being a more dominant strategy than gonochorism (Goffredo 2000). In cyclical hermaphroditism, a single individual is unable to produce viable gametes of both sexes at the same time, so self fertilisation cannot occur. Selfing is thought to be an important mode of reproduction in hermaphroditic corals that can ensure fertilisation success (Brazeau et al. 1998); however, it does not allow for genetic diversity and evolution of a species (Veron 1995).

The large egg size of these three species suggest lecithotrophic rather than planktotrophic early development (Fadlallah 1983; Gage and Tyler 1991). Lecithotrophic development, contrary to earlier suggestions, is now recognised as a beneficial adaptation for wide dispersal in oligotrophic environments, such as the deep sea (Shilling and Manahan 1994). Most deep-sea scleractinians studied to date (seven out of eight species) appear to have lecithotrophic larvae (Waller et al. 2002; Waller and Tyler (in press); Burgess and Babcock (2005)). Though planulation in deep-sea species is difficult to observe without in vitro cultures, histological evidence suggests that all three species of *Caryophyllia* in this study spawn gametes rather than brood. This is inferred by both the lack of planulae and the varying stages of gamete development within the population (which would mean that the likelihood of observing planulae within the polyp would be high). The spawning of gametes as the normal mode of reproduction in the Cnidaria has been well documented for a number of shallow species of coral (Kojis and Quinn 1982; Bothwell 1982; Fadlallah and Pearse 1982a, 1982b; Fadlallah 1983; Harrison et al. 1984; Szmant 1986; Harrison and Wallace 1990; Richmond and Hunter 1990; Richmond 1997). *C. smithii*, a shallow-water congeneric, also broadcast spawns and is externally fertilised (Tranter et al. 1982), although there is a report of possible brooding (Hiscock and Howlett 1977). Rinkevich and Loya (1989) proposed that large-polyp species would be unlikely to brood, as the extra energy required for growth, defence, and maintenance of the large polyp would mean that the energy required to produce a brooded planulae would be unavailable. Stimson (1978) also suggested that deep fore-reef scleractinians may broadcast gametes in order to aid the wide dispersal distance required at depths. These two theories fit with the data acquired during this study. All of these *Caryophyllia* species broadcast gametes, and the average oocyte size increases with polyp size.

Gametes of shallow-water scleractinians are thought to develop within the lamellae of the mesenteries and subsequently migrate into the mesoglea, to develop as oogonia (Szmant-Froelich et al. 1980; Fadlallah 1983). Of all three species of *Caryophyllia* studied here, oogonia and spermatocysts were first observed attached to the mesenterial lamella, and so this mode of development is also believed to be the case with these deep-water corals. This has also been observed in other species of deep-water scleractinian, i.e., *Fungiacyathus marenzelleri* (Waller et al. 2002), *Lophelia pertusa*, and *Madrepora oculata* (Waller and Tyler, accepted).

Caryophyllia smithii is gonochoric and a seasonal reproducer, producing gametes between January and March (Tranter et al. 1982). This is a very different strategy from the three deep-water species examined in this study even though they are all congeners. It is not unusual for scleractinian species within the same genus to have differing reproductive patterns (Fadlallah 1983; Harrison and Hunter 1990) and so it is possible that this change in reproductive strategy is environmentally, rather than phylogenetically, constrained.

Both the average fecundity and average oocyte size (although this pattern is not apparent in *C. smithii*) increase with depth in these three species of deep-water *Caryophyllia* (Table 2). Spawning and larval type also

Table 2 Comparisons of depth range and reproductive ecology of four species of Caryophyllia

Species	Depth	Max oocyte diameter	Max fecundity (per polyp)	Sex	Gamete release	Larvae type
**C. smithii*	2–1200 m	150 μm	'several thousand'	Gonochoric	Seasonal	Planktotrophic
C. cornuformis	435–2000 m	350 μm	N/D	(Cyclical) Hermaphrodite	(Quasi continuous)	(Lecithotrophic)
C. sequenzae	960–1900 m	430 μm	940	Cyclical hermaphrodite	Quasi continuous	(Lecithotrophic)
C. ambrosia	1100–3000 m	700 μm	2750	Cyclical hermaphrodite	Quasi continuous	(Lecithotrophic)

**C. smithii* data from Tranter et al. 1982
N/D = No data; hypothesised data are represented in parenthesis

appear to shift between seasonal planktotrophic to quasi-continuous lecithotrophic development as the depth increases. Environmental conditions have often been shown to influence reproductive strategies. Many species of shallow scleractinians have been shown to use lunar periodicity and seasonal temperature differences to time their reproduction (Fadlallah 1983; Richmond 1997), whereas reproduction in several deep-water invertebrate species may be cued in the NE Atlantic by a seasonal phytodetrital pulse (Billett et al. 1983; Tyler et al. 1992; Tyler et al. 1993). Brooding was also originally thought to be an ideal strategy for the deep-sea environment as it takes a developing planulae to late stages before releasing it to the 'harsh' environment (Gage and Tyler 1991), though this pattern is yet to be found in the deep-sea Anthozoa.

The asynchronous pattern of reproduction observed in these three species suggests that there is a near constant presence of spawned gametes in the water, while it remains possible that individuals in close proximity to one another are synchronously spawning. Because individuals were trawled, their small-scale spatial distribution is not known. There are also no data available on the density of any of the deep-water *Caryophyllia spp.* corals. Densities of both individuals and gametes in broadcast spawning species must be sufficiently high to allow successful fertilization, yet because of low food availability, densities of fauna are generally regarded as low in the deep sea (Gage and Tyler 1991). Population densities of deep-water solitary corals are likely to play an extremely important role in their reproductive strategies and ecology.

Acknowledgements This research was supported by the European Union 'Atlantic Coral Ecosystem Study' contract no. EVK3-CT1999-00008. For sample collection we would like to thank the Captains and crew of the RRS *Challenger*, RRS *Charles Darwin*, and the RRS *Discovery*. Peter Lamont and Murray Roberts also provided invaluable assistance in obtaining samples from DML, Oban. We would also like to thank three anonymous reviewers for useful comments and suggestions that greatly improved this mnauscript.

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